gesting that an extremely tight connection occurs between the epithelium and cuticular flange. These examples suggest that a tight connection occurring at the muscle attachment to the hard exoskeleton is a common condition among different animals.

Why does *Nautilus* develop such a curious muscle-shell attachment system? How is it effective in relation to the mode of life and ontogenetic growth? The nektonic mode of life in *Nautilus* may be a key to assuming these questions. Most other externally shelled mollusks are benthic. When benthic mollusks perform various actions such as valve opening and closing, or crawling on and burrowing into substratum, they bear their own weight on the muscular system. In such situations, the myoadhesive epithelium functions as tendon because it receives a large tensile stress caused by muscle movement. In other words, in benthic mollusks, a tight connection between the internal shell wall and the myoadhesive cells appears to be necessary to sustain the large tensile stress. On the contrary, *Nautilus* maintains neutral buoyancy in the water column by means of a chambered shell filled with low-pressure gas and small amounts of liquid. Therefore, the tensile stress bearing the myoadhesive cells may be relatively reduced in this animal.

Another factor is the mode of mantle shifting through the inside of the body chamber during growth. In *Nautilus*, the formation of a new chamber is episodic. At the stage of a new chamber formation, the septal myoadhesive band is rapidly moved forward in the body chamber, where it reattaches to the internal shell wall (Ward & Chamberlain, 1983). It is suggested that a loose connection between the epithelium and the semi-transparent membrane lining the inner wall of the body chamber may be effective for the alternating mode of peeling off and reattachment of the septal myoadhesive band. By contrast, the shift of the attachment site for the retractor muscle corresponds to the apertural shell growth, which is constant throughout new chamber formation (Ward & Chamberlain, 1983). However, there are no structural differences between the retractor and septal myoadhesive cells based on light microscopic observations. Having a loose attachment of the epithelium to the shell might also be a favorable condition for moving of the myoadhesive cells because they appear to shift more than 30 centimeters throughout ontogeny, whereas the expansion rate of the lateral termination of the muscle seems to be considerably smaller as compared with that of other mollusks.

As pointed out above, the nektonic mode of life and the mode of shell growth in combination with the chamber formation cycle during ontogeny in *Nautilus* are unique among mollusks. Therefore, the muscle-shell attachment in *Nautilus* might have developed as a response to its own functional demands. If the mechanism of muscle-shell attachment in mollusks is highly constrained by mode of life and shell growth, a similar mechanism might occur even in distantly related taxa. In fact, all mollusks hitherto examined excluding *Nautilus*, are sessile or mobile benthos. Thus, there is a possibility that nektonic and planktonic mollusks such as janthinid, pteropod, and heteropod gastropods have a similar mechanism of muscle-shell attachment to that observed in *Nautilus*.

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Range Extensions of Sacoglossan and Nudibranch Mollusks (Gastropoda: Opisthobranchia) to Alaska

JEFFREY H. R. GODDARD

Marine Science Institute, University of California, Santa Barbara, California 93106, USA

AND

NORA R. FOSTER

University of Alaska Museum, Fairbanks, Alaska 99701, USA

Abstract. Range extensions to or within Alaska are described for 16 species of opisthobranch mollusks. The ranges of nine of these, including the sacoglossans *Alderia modesta* and *Olea hansineensis* and the arminacean nudibranch *Janolus fuscus*, are extended northward from British Columbia or southeast Alaska. The ranges of another five species, including four dorids and the arminacean *Armina californica*, are extended westward from sites within Alaska. The range of an arctic species, *Calycidoris guentheri*, is extended southward into the central Bering Sea, and that of the circumboreal *Palio dubia* northeastward to south-central Alaska. Given the circumboreal or amphi-Pacific distributions of about half of these species, as well as the paucity of previous observations in much of Alaska, we consider most, if not all, of these range extensions the result of increased or fortuitous search efforts, rather than actual range expansions by the species themselves.

INTRODUCTION

Lee & Foster (1985) reviewed the literature and summarized the known records of opisthobranchs from Alaska, greatly expanding our knowledge of the fauna from the Gulf of Alaska, Bering Sea, and Arctic Ocean. More recently, Foster (1987a, b), Millen (1989), Behrens (1997, 1998), and Goddard (2000) extended the ranges of additional species to southeast and south-central Alaska; and Millen (1985, 1987) synonymized several species of onchidoridid nudibranchs reported from Alaska. Since these reports, we have continued our studies of the opisthobranch fauna of Alaska, focusing especially on sites on the Kenai Peninsula and in Prince William Sound during surveys of non-indigenous marine species led by researchers from the Smithsonian Environmental Research Center (SERC) (Hines et al., 2000). In addition, we have examined specimens collected by other researchers and deposited in the University of Alaska Museum since 1985. As a result of these studies, we have extended the known ranges of two sacoglossans and 14 nudibranchs to or within Alaskan waters. This paper documents these range extensions and discusses some of their biogeographic implications.

STUDY SITES AND METHODS

We searched for opisthobranchs at sites on the Kenai Peninsula and in Prince William Sound (Figure 1, Table 1), during June and September 1998, August 1999, and July 2000. We collected specimens by hand from intertidal mudflats and rocky shores, floating docks and buoys, rock jetties, and from settling plates deployed in the shallow subtidal by personnel from SERC earlier in the year. We used a dissecting microscope or hand lens to observe specimens alive, and then fixed them in either 5 to 10% formalin or 70% ethanol. Specimens not identified in the field, or those collected by other workers and already deposited in the University of Alaska Museum, were examined, dissected, and identified in the laboratory at either the University of California at Santa Barbara or the University of Alaska in Fairbanks. We deposited voucher specimens in the University of Alaska Museum (UAM) in Fairbanks or in the California Academy of Sciences invertebrate zoology collection (CASIZ) in San Francisco. Catalogue numbers for these are given with the species accounts below.

RESULTS

We extended the known ranges of 16 species: nine species northward from British Columbia and southeastern Alaska, five species westward from sites within Alaskan waters, one species northeastward from the Aleutian Islands, and one species southward within the Bering Sea. These species are listed below (alphabetically within each higher taxon) with notes on their classification, habitats, and prey.

In addition to the following species, we also found *Cuthona albocrusta* (MacFarland, 1966) on floating docks

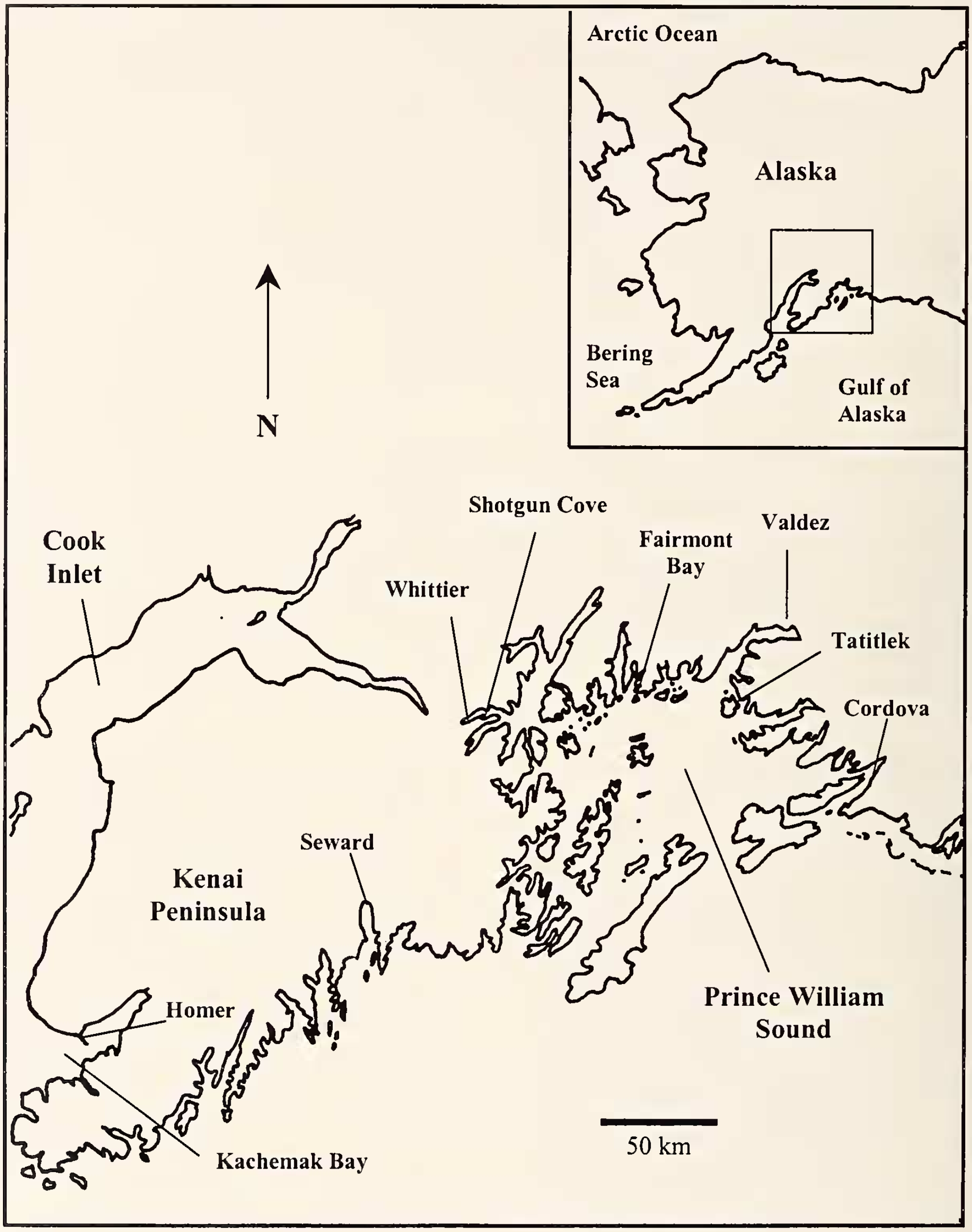

Figure 1. Map of the Kenai Peninsula and Prince William Sound, Alaska, showing location of the study sites.

in Cordova, Prince William Sound (Figure 1). Goddard (2000) reported this range extension from southern British Columbia, but we only recently deposited the specimen on which that range extension was based in the California Academy of Sciences (CASIZ 146069).

Sacoglossa

Alderia modesta (Lovén, 1844)

Adults and their egg masses were abundant on the yellow-green alga *Vaucheria* sp. on the high intertidal mudflats immediately southwest of the Cordova marina on 13 August 1999. We have deposited three specimens in the California Academy of Sciences (CASIZ 142448). This is a range extension of 1620 km northwest from Port Alice, Vancouver Island, British Columbia (Millen, 1980).

Millen (1980:1209) noted that *Alderia albopapillosa* Dall, 1871, collected by Dall (1871) from Sitka, Alaska, might be synonymous with *A. modesta*. However, as pointed out by Hand & Steinberg (1955:26), Bergh

Table 1

Location of study sites for opisthobranch gastropods in south-central coastal Alaska.

Site	Latitude (N)	Longitude (W)
Cordova	60°32.50′	145°46.47′
Fairmont Bay	60°53.05′	147°23.52′
Hanning Bay, Montague Island	59°57′	147°46′
Homer spit marina	59°37.97′	151°26.17′
Little Takli Island	58°04′	154°29′
Port Etches, Hinchinbrook Island	60°13′	146°42′
Seward	60°07.43′	149°22.72′
Shotgun Cove	60°47.43′	148°32.50′
Tatitlek	60°52.10′	146°43.47′
Valdez	61°07.42′	146°21.25′
Whittier	60°46.62′	148°41.40′

(1880) showed that Dall's specimens of *A. albopapillosa* actually belonged to the dorid nudibranch genus *Adalaria.* Millen (1987) later synonomized *Adalaria albopapillosa* (Dall, 1871) with *Adalaria proxima* (Alder & Hancock, 1854), but did not mention its previous and short-lived placement in the genus *Alderia.*

Olea hansineensis Agersborg, 1923

One specimen (CASIZ 142449) of this opisthobranch egg-eating sacoglossan was found on an egg mass of the cephalaspidean *Melanochlamys diomedea* (Bergh, 1894) on the mudflat southwest of the Cordova marina on 13 August 1999. This is a range extension of 1825 km northwest from Sechelt Inlet, British Columbia (Millen, 1980).

Nudibranchia, Doridacea

Adalaria jannae Millen, 1987

This species was abundant, along with its ribbon-shaped egg masses, on the encrusting bryozoan *Membranipora* sp. growing on the kelp *Laminaria* sp. on floating docks at Whittier and on a moored buoy in Shotgun Cove, both on 10 August 1999. Owing to the influence of glaciers and snow fields in the fjord surrounding Whittier, the salinity (and temperature) of the surface water in the marina was very low, and we found nudibranchs, their prey, and other fouling invertebrates at this site only on *Laminaria* growing below the fresh water lens. *Adalaria jannae* closely resembles *Onchidoris muricata,* but lacks the medial radular teeth found in the latter; *A. jannae* also has four to six small lateral teeth on each half row of the radula, as well as ribbon-shaped egg masses (Millen, 1987). The radular formula from an 8 mm-long (preserved) specimen from Shotgun Cove was 30 × 4.1.0.1.4. Eight specimens from Whittier have been deposited in the California Academy of Sciences (CASIZ 142450). This is a range extension 1745 km northwest from Sointula, British Columbia (Millen, 1987).

Adalaria sp. 1 of Behrens (1991) and Millen (1987:2701)

One specimen (CASIZ 142451), 3.3 mm long (preserved) was found on the low intertidal rocky shore at Tatitlek on 12 August 1999. The morphology of this specimen matched that of specimens observed by one of us (JHRG) in Oregon and Washington (Goddard, 1984, Goddard et al., 1997). This is a range extension of 1080 km northwest from Ketchikan, Alaska (Millen, 1989).

Ancula pacifica MacFarland, 1905

A single specimen (CASIZ 142452), lacking orange lines on the body, was found on the floating docks in the Cordova marina on 13 August 1999. This species (or just the color form of *A. pacifica* lacking orange lines on the body) may be a junior synonym of *Ancula gibbosa* (Risso, 1818), which is known from the north Atlantic Ocean and Barents Sea (McDonald, 1983; Thomson & Brown, 1984). This is a range extension of 1080 km northwest from Grant Island, Ketchikan, Alaska (Millen, 1989).

Archidoris odhneri (MacFarland, 1966)

One specimen (UAM 7153) was collected from unknown depth by R. Baxter 31 January 1985 using a bottom trawl on the continental shelf off the north side of the Alaska Peninsula (57°00′N, 162°03.40′W) in the Bering Sea. This is a range extension of 660 km southwest from Port Dick on the Kenai Peninsula, Alaska (Robilliard & Barr, 1978).

Calycidoris guentheri Abraham, 1876

One specimen (UAM 7154) was collected from unknown depth by R. Baxter 2 September 1985 using a bottom trawl on the continental shelf in the central Bering Sea (57°17.68′N, 178°20.15′W). This is a range extension of 1250 km southwest from the Bering Strait (Lee & Foster, 1985).

Diaulula sandiegensis (Cooper, 1863)

One specimen (UAM 7155) was collected from unknown depth by R. Baxter 9 October 1986 using a bottom trawl in the central Aleutian Islands (52°21.44′N, 179°49.23′W). This is a range extension of 850 km west from Unalaska Island (Bergh, 1894).

Doridella steinbergae (Lance, 1962)

Foster (1987a) extended the range of this species from Bamfield, Vancouver Island, British Columbia to Prince William Sound, Alaska. During the present study we found 12 specimens of *Doridella steinbergae,* 1 to 5 mm long, on its prey, *Membranipora* sp., on drift kelp *Laminaria* sp. on the mudflats at Cordova on 13 August 1999 (CASIZ 146077). We also found this species on *Laminaria* sp. in the low rocky intertidal zone at Little Takli Island, Katmai National Park on 27 July 1998, extending its range 475 km southwest from Prince William Sound (Foster, 1987a).

Geitodoris heathi (MacFarland, 1905)

Four specimens were found on the low intertidal rocky shore at Tatitlek on 12 August 1999; three of these have been deposited in the California Academy of Sciences (CASIZ 142453). This is a range extension of 1080 km northwest from Ketchikan, Alaska (Millen, 1989).

Palio dubia (M. Sars, 1829)

Adults and egg masses (CASIZ 142454) were abundant on the bryozoan *Membranipora* sp. growing on the kelp *Laminaria* sp. on the floating docks at Whittier on 10 August 1999. Additional specimens were found on the buoy at Shotgun Cove on 10 August 1999 and on the docks at Cordova on 13 August 1999. Our specimens were uniformly translucent light brown in color, with delicate and flaccid bodies, and had five branchial plumes. The rhinophores on one specimen had 12 lamellae. The radula from another specimen had a formula of $15 \times 5.2.0.2.5$, with the marginal teeth ranging in size from (inner to outermost) 135 to 45 μm high by 50 to 10 μm wide. These characters closely match those of *P. dubia* described by Thompson & Brown (1984) and Picton & Morrow (1994). They also match Bergh's (1880) description of *P. pallida.* Thompson & Brown (1984) consider the latter a junior synonym of *P. dubia;* we concur. The specimens from Cordova represent a range extension of 2450 km northeast from Kiska Island in the Aleutians (Bergh, 1880). *Palio dubia* has also been recorded from the northern Sea of Japan (Martynov, 1998a).

Triopha catalinae (Cooper, 1863)

One specimen (UAM 7156) was collected by C. Simenstad from 6 m depth on 30 June 1987 off Shemya Island (52°43.33′N, 174°07.00′E) in the Aleutians. This is a range extension of 360 km northwest from Amchitka Island (Robilliard, 1974).

Nudibranchia, Arminacea

Armina californica (Cooper, 1863)

One specimen (UAM 7157) collected from unknown depth by R. Baxter on 23 September 1986 using a bottom trawl off the north side of Akutan Island (54°16.9′N, 165°57.09′W) in the Aleutian Islands. This is a range extension of 1450 km southwest from Kayak Island in the Gulf of Alaska (Lee & Foster, 1985). Additional specimens (UAM 7158 & 7159) were collected by one of us (NRF) in March 1986 from between 102 and 140 m depth in Hanning Bay, Montague Island and between 55 and 129 m in Port Etches, Hinchinbrook Island. Both of these latter sites are in Prince William Sound (Table 1).

Janolus fuscus (O'Donoghue, 1924)

Two specimens, 60 and 70 mm long, of this distinctive species were found with their egg masses on the bryozoan *Bugula* sp. on floating docks in the Homer marina at the mouth of Kachemak Bay on 8 August 1999. We returned these specimens to their habitat after making our observations, confirming their identity, and showing them to others members of the SERC survey team. This is a range extension of 1250 km northwest from Klu Bay, Revillagigedo Island, southeast Alaska (Robilliard & Barr, 1978).

Nudibranchia, Aeolidacea

Cuthona pustulata (Alder & Hancock, 1864)

Four specimens (CASIZ 146070), 4 to 5 mm long, were found feeding on the hydroid *Sarsia* sp. on a dock in the marina at Homer on 8 August 1999. These specimens resembled Gosliner & Millen's (1984) description of *Cuthona pustulata* from British Columbia, especially with regard to overall shape of the body, cerata, and head tentacles. However, our specimens were smaller than those examined by Gosliner & Millen (1984) and differed by lacking large white spots on the cerata (they did have smaller opaque white flecks). They also had slightly fewer rows of cerata (six to eight compared to eight to 14), with fewer cerata per row (one to three, compared to two to eight reported by Gosliner & Millen (1984) for a 16 mm-long specimen). The radula and shape of the radular teeth of our specimens were virtually identical to that described by Gosliner & Millen (1984) but differed in having four to five lateral denticles, instead of five to nine. These specimens represent a range extension of 2160 km northwest from Galiano Island, British Columbia (Gosliner & Millen, 1984).

Eubranchus olivaceus (O'Donoghue, 1922)

We found 10 specimens with their egg masses on the hydroid *Obelia* sp. growing on floating docks in the Homer marina on Kachemak Bay on 8 August 1999 (CASIZ 146071). We found an additional specimen on *Obelia* sp. on docks at Whittier on 10 August 1999. The body of these specimens was translucent with small epidermal flecks of either encrusting white or encrusting reddish brown. The cerata, but not the rhinophores or cephalic tentacles, had a subterminal band of encrusting brown pigment. On some specimens, encrusting white pigment was concentrated distally on the rhinophores and cerata. The cerata cores and the branches of the digestive gland